

**Mating Strategies in a Darwinian Microworld:
Simulating the Consequences of
Female Reproductive Refractoriness**

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ABSTRACT

Characteristic sex differences in mating strategies (e.g., choosy females; unselective males) have been claimed by Trivers and other theorists to evolve as an automatic consequence of sex differences in minimum parental investment, arising chiefly from greater female reproductive refractoriness. The theory has been supported by correlational evidence and conceptual analogies to economics. A simulated evolution experiment was performed to provide a clearer test of whether female reproductive refractoriness alone can drive the emergence of differences in mating selectivity. A population of male and female replicators initially differed only in that females were unavailable to mate for a fixed period prior to the appearance of offspring. Over succeeding generations, females evolved far greater selectivity than males with respect to the longevity of potential mates. This greater selectivity was relatively robust with respect to population and genetic parameters, but quantitatively unstable with realistic breeding population sizes.

Darwin observed that in virtually all animal species, males and females exhibit different mating behaviors. Males are usually relatively indiscriminate in their mating choices and they often fight among each other for access to mates. Females are usually relatively choosy in selecting mates, and they rarely fight other females for access to mates. In some species, males present “gifts” to females in order to secure copulation. Like me any other observers, Darwin was puzzled by these phenomena, and he was unable to find a satisfactory explanation for them.

Evolution of Mate Choice

Extending suggestions of Bateman (1949) and Williams (1966), Robert Trivers (1972) proposed what has come to be the most widely accepted explanation for these phenomena within a Darwinian framework. According to Trivers' account, sometimes referred to as *parental investment theory*, the underlying variable ultimately responsible for behavioral differences between males and females is a difference in the minimum investment that a male and a female might potentially make in a surviving offspring. The term ‘investment’ encompasses all limited resources, including time (gestation, parental care) as well as metabolic and material resources. In most species, the minimum male parental investment is a small amount of time and a small metabolic cost. By contrast, the female is subject to substantial reproductive refractoriness, and the

minimum female parental investment is typically quite large (often including energy and risk as well as the required temporal investment). According to Trivers, the fact that offspring are invariably costly for females entails that female reproductive capacity is a limited commodity. This, according to the theory, automatically puts females in the position of choosers, thereby commanding a resource for which males will compete.

Starting with Trivers (1968), many writers have cited observations about so-called “sex-role reversed species” as supposedly clinching the argument for the parental investment account (e.g., Daly and Wilson, 1983; Alcock, 1989). In these species, such as the giant water bug *Abedus herberti* and the sea horse *Syngnathidae*, males shoulder most of the burden of parental care. Females of these species have been reported to be less discriminating than males in choosing mates, with males sometimes even described as “coy” (e.g., Fiedler, 1954)

While the observations with sex-role reversed species appear consistent with theory, it is not clear that they provide compelling evidence for it. After all, sex-role reversed species are anomalous with respect to numerous mating-related behaviors and even morphology. The fact that a handful of species are anomalous with respect to two features -- parental investment and sexual selectivity – among others is essentially a correlational observation (and one of dubious reliability given the tiny sample size). As is well known, correlational evidence cannot specify which of many variables is causally fundamental. For example, it is possible that the choosiness difference might drive the differences

in investment, rather than the reverse. Thus, there would seem to be little reason to regard the sex-role reversal data as providing overwhelming evidence for Trivers' theory.

Perhaps a more compelling reason to accept Trivers' interpretation is the widespread intuition that natural selection must inevitably produce such a difference in selectivity given an ineradicable difference in minimum possible investment. This assumption is sometimes bolstered by intuitive verbal arguments that invoke analogies to economics (e.g., Trivers, 1972; Alcock, 1989; Daly and Wilson, 1983). While these arguments sound persuasive, if scrutinized they can be seen to introduce (sometimes rather slyly) the assumption that mate choice will involve something analogous to an auction in which individuals can choose the fittest available mate from a pool of candidates. Given this assumption along with a few others, one might construct a sort of proof that the more scarce sex will command a higher "price" in fitness than the more common sex. Since female reproductive refractoriness will drive down the number of available females, the evolution of choosiness might seem to follow. However, the argument relies on the assumption of an auction, and this assumption is overly restrictive. While in some species one sees leks (meeting grounds at which females pick from a number of suitors) these are by no means universal. More significant is the question of whether natural selection will inexorably drive the evolution of greater female selectivity even when individuals are unable to engage in any kind of adaptive or relative mate choice.

More generally, purely verbal reasoning should probably be regarded with some skepticism when it comes to the behavior of complex nonlinear systems; even the relatively rigorous method of stochastic analysis of selection pressure at equilibrium can seriously mischaracterize the behavior of such systems (see Fogel, Fogel, & Andrews, 1997 for an example).

In the present article, we examine the contribution of parental investment differences to mating strategy differences using simulated evolution of populations of artificial organisms. Previous research using simulation to shed light on mating systems has examined sexual selection (Collins & Jefferson, 1992; Miller & Todd, 1993; Werner, 1996) and the evolutionary pressures governing honest and dishonest signaling (Bullock, 1998; Noble, 1999). In designing the present simulation, an effort was made to include all and only those features of animals that should be strictly necessary according to a Trivers-type analysis. These include: greater female reproductive refractoriness, sex-linked inheritance of fitness-relevant traits, sexual selection, sex-linked inheritance of mechanisms for discriminative mating, intra-specific competition for mates, natural selection, and the least restrictive mate-choice scheme: “historyless” acceptance or rejection of suitors based on a genetically fixed fitness threshold. The theory implies that the many other features of the animal world besides the ones listed above play no essential role in the evolution of these sex differences. For example, none of the following should be critical: leks or any other mechanism for choosing the best available mate, mate selection criteria that are modifiable by experience, parental care and its Darwinian costs,

a high dimensional genome, a diploid genome, high organismal complexity, low mutation rates, and multidimensionality of fitness (disease resistance, fecundity, etc.). By testing whether mating strategy differences prove to be robust in simulations lacking all of these features, we test the claim (implicit in Trivers' theory) that none of the features on this list play a critical role in producing these differences.

Simulation Approach

The simulations described here involve a highly simplified model of a haploid organism with genetically determined fitness. The organisms exhibit heritable sex-linked variation in two traits: longevity and mating selectivity (willingness to mate with potential mates conditionalized on the potential mate's fitness). To provide a critical test of the sufficiency of Trivers' analysis, only one sex difference was "wired into" the population at the outset of the simulations: female reproductive refractoriness. Before producing an offspring, a female replicator was obliged to "sit out" a fixed amount of time before being able to mate again. Aside from this, the distribution of all parameters for males and females was equated at the outset. Sex-linked inheritance afforded the opportunity for sex differences to emerge as the simulation was run for thousands of generations, but the direction of any such difference was not dictated by the structure of the model.

Our initial question was straightforward: do sex differences in mating selectivity emerge automatically as a consequence of female reproductive

refractoriness, as Trivers' analysis implies? If so, are the selectivity differences stable and does their magnitude depend on parameters such as the duration of female reproductive refractoriness or the rate of mutations?

Simulation Methodology

Genome. The genome of each organism consisted of genes encoding two sex-linked attributes (as described below):

1. Longevity. The longevity of an organism was represented as a binary value (short versus a long-lived variant). The lifespans of each variant was adjustable.
2. Selectivity. Each organism had encoded within its genes a probability of agreeing to mate with any potential mate conditional on the longevity of that potential mate. For a given longevity level, this was represented as a real number in the range (0,1). Selectivity was initially assigned randomly with real values selected between 0.49 and 0.51, randomly chosen without regard to sex. One may view this real-numbered value as the model's representation of a graded polygenic trait.

All traits were sex-linked in the following way. Consider a male organism. At any given locus, the organism possessed two genes, one coding the value of the trait to be expressed if the organism was male, the other coding the value expressed if the organism was female. A male's longevity depended only upon

his male-linked allele. If this male had a daughter, she would inherit his female-linked allele with probability 0.5; otherwise, she inherited her mother's female-linked allele. Inheritance of different genes was independent, i.e., there was no linkage between different genes. This simplified form of sex-linked inheritance does not capture the full complexities of sex-linked inheritance in real organisms, but should capture the features that are essential according to Trivers' analysis.

Mating. Time unfolded in discrete time-steps. On a given time-step, each individual potentially available to mate was paired with a randomly chosen candidate of the opposite sex; if there was an excess of one sex, a randomly chosen subset of individuals of the more common sex sat out the time-step. On a given time-step, each individual presented with a potential mate might or might not agree to mate with the potential mate. The probability a mating would occur was a genetically specified function of both mates' longevity and choosiness, and mating took place if and only if both potential mates agreed. Suppose male M_i and female F_j , both of longevity 0, encounter each other on timestep t , and M_i has a probability .6 of mating with a candidate mate of longevity 0, while F_j has a probability .7 of mating with a candidate mate of fitness 0. In this case, mating would occur on timestep t with a probability 0.42 ($.6 * .7$). If the individuals paired up did not mate, they were ineligible to mate on the present time-step but became eligible again on the next time-step (assuming they survived).

Reproduction. For computational convenience, the population had a fixed carrying capacity, and slots for new offspring opened up whenever an individual died. Whenever two individuals mated, an offspring was created unless the carrying capacity of the population had been reached (in which case all mating ceased on that time-step).

Each allele in a male offspring randomly received (with probability .5) either the father's (expressed) male-linked allele or the mother's (latent) male-linked allele at that locus. Each allele in a female offspring received either mother's (expressed) female-linked allele or the father's (latent) female-linked allele at that locus. The binary-valued fitness alleles were "flipped" with a fixed probability (fitness-mutation probability parameter). The real-valued selectivity genes were subject to real-valued mutation: addition of a Gaussian random variable with a mean zero and a standard deviation determined by the selectivity mutation parameter.

When an offspring was produced, the female was ineligible to mate for a fixed number of time-steps (the female reproductive refractoriness parameter); males could always mate again on the next time step. The new offspring did not enter the population until this period had elapsed (thus, the reproductive refractoriness corresponded to gestation). The parameters of the simulation are listed in the Table 1, along with the range explored.

Results and Discussion.

Robust Qualitative Findings.

As already noted, at the outset of the simulations, males and females had the same initial distribution of longevity and selectivity parameters; the only “hardwired” sex difference was the inability of females to mate for a fixed number of time-steps after producing an offspring (the female reproductive refractoriness parameter).

INSERT FIGURE 1

Figure 1 shows the changes in longevity for a representative simulation of 150,000 timesteps, with lifespans of 15 and 25 time-steps (for short- and long-lived variants, respectively), and relatively large female reproductive refractoriness (4 timesteps); the parameter values that produced these results are listed in Table 1. The results of this simulation illustrate two qualitative findings that proved robust with respect to the choice of parameter values. The first is rather obvious: for both males and females, the initially equal distribution of short- and long-lived individuals rapidly gave way to a preponderance of long-lived individuals. This reflects the combined effects of natural and sexual selection. Second, note that the excess of long-lived over short-lived individuals is greater among males as compared to females. This reflects the fact that males are subject to more intensive sexual selection than females, as will be

discussed shortly. This is demonstrated by the fact that when the simulation was re-run with the mechanisms for discriminative mating eliminated, the male and female fitness distributions appeared identical after 150,000 timesteps.

Selectivity Changes.

The key question was whether and how evolution would alter selectivity. Figures 2 and 3 shows the evolution of mating selectivity in males and females for the parameter values shown in Table 1 (Figure 2 shows two representative runs, while Figure 3 shows the mean parameter values of 16 simulations at 150,000 timesteps, along with standard deviations for these values). The overall pattern was quite replicable: Male willingness to mate with low- and high-fitness potential mates rose rapidly, and by about 25,000 timesteps these values appeared to have reached asymptotic levels, with males showing only a modest preference for mating with long-lived mates (modest at least as assessed by the ratio of the probability of mating given a potential long-lived mate divided by the probability of mating with a short-lived mate). Female willingness to mate with long-lived males increased fairly rapidly, too, but rarely reached as high a level as the corresponding value for males in any of our simulations. Female willingness to mate with short-lived males, on the other hand, usually showed a small and temporary rise and then fell to a level far below the other mating probability values.

INSERT FIGURES 2 AND 3

The relative robustness of greater female selectivity clearly confirms Trivers' essential claim that a reproductive refractoriness difference is by itself sufficient to force the evolution of a greater female selectivity for genetic quality of mates. The fact that females never show the same willingness as males have to mate with high-quality mates was unexpected, however.

The results also a degree of instability in the female probability of mating with a low-fitness male that was not anticipated. This is seen in the representative runs shown in Figure 2, and also in the high standard deviations across runs shown in Figure 3. At first we assumed that this parameter had not reached a stable state, but simulations out to 500,000 time-steps disclosed no obvious stabilization. The instability was affected by mutation rates, as described below, but we did not find any parameter values that produced much more stable preferences than those seen in Figure 2. It appears likely that this instability reflects probabilistic sampling error rather than limit cycles, because it was reduced by modifying the simulation to contain much a larger (probably unrealistically large) interbreeding population¹.

Parameter Dependence.

Male reproductive refractoriness was always set to zero (meaning that males were always available to mate on the next time step), but the female

temporal investment was varied between 2 and 6. Increasing female reproductive refractoriness substantially amplified the sexual dimorphism in evolved mating selectivity. This is seen in Figure 3, which shows the average probability of a female being willing to mate with a male of low fitness, averaged over three runs of the simulation for 150,000 timesteps with mutation probability 0.1. The figure discloses a striking and nonlinear effect of reproductive refractoriness upon female mating strategy; while some degree of dimorphism was evident at all values of female reproductive refractoriness, increasing the refractoriness from 3 to 4 abruptly increased the effect as assessed by mean female probability of mating with a short-lived mate. The greater average fitness of the male population emerged at the same point, confirming that this difference was generated by sexual rather than natural selection.

INSERT FIGURE 4

The mutation rate for the longevity gene was varied between 0.001 and 0.4. When the rate was 0.2 or higher, the difference in female and male selectivity waned, with both sexes evolving an indiscriminate willingness to mate regardless of a prospective mate's fitness. This may be explained by the fact that extreme mutation rates attenuate the heritability of longevity itself – and along with it the potential gain to be had by choosing a long-lived mate. When the mutation rate was set to 0.001 or below, on the other hand, the evolved

¹ An anonymous reviewer of an earlier version of this manuscript pointed out that female reproductive refractoriness reduces the selection pressure on the females' willingness to mate,

selectivity values appeared even more unstable than those shown in Figure 2. The long-term averages appeared similar to those shown in the figure, but male as well as female selectivity values showed massive drift over tens of thousands of timesteps. It is possible that larger population sizes could compensate for this, although we have not explored this possibility.

Contrasts with Biological Evolution.

While the results of the simulation make it clear that differential reproductive refractoriness alone suffices to drive the evolution of sex-linked differences in mating strategies, it should be noted that the design of this model facilitated this emergence by positing sex-linked inheritance of selectivity. It would be interesting to carry out similar experiments with a model structure that allows both sex-linked and non-sex-linked inheritance of longevity and selectivity to evolve. Based on Trivers' analysis, one should expect that sex-linked inheritance would be "chosen" over non-sex-linked inheritance, a point the present results have not shown.

As pointed out above, several features of the model appear unrealistic from a biological perspective, and some of these differences deserve comment. First, the mutation rates explored here exceed plausible estimates for living organisms by at least several orders of magnitude (see Maynard Smith, 1999, for discussion). As noted above, when a mutation rate much below 0.001 is used, the basic patterns described here emerge but they appear far less stable. We conjecture that this is because the low-fitness alleles become so rare that the

which may contribute to this instability.

“risks” of unselective mating are attenuated. Consequently, selectivity and sex differences in selectivity cease to be under strong evolutionary control, and neutral drift becomes more important.

One may ask why it should be necessary to use an unrealistically high mutation rate in order to see a preference for “good genes” evolve. Is a preference for good genes such a fragile phenomenon? Perhaps not. It may be relevant here that the genome of these simulated organisms is unrealistically tiny. Sexual selection in nature that worked to disadvantage bearers of deleterious mutations would undoubtedly have to discriminate against a vast number of potential mutations, each of which occurs at an extremely low rate. Thus, the “short-lived” allele in the present model may be seen as a discrete and unitary proxy for overall genetic unfitness; understood in this way, the conclusions of the model regarding mutation rates may actually be quite pertinent to evolution in living organisms. While one could simulate replicators with a realistic-sized genome and a realistically low incidence of individual deleterious mutations, it seems likely that this would end up mimicking the present simulation rather than adding anything to it.

Another feature of this simulation that seems unrealistic relates to longevity. The simulation generated strong natural and sexual selection for lifespan. However, longevity per se is not normally considered synonymous with “good genes” nor is it generally assumed that greater lifespan is typically favored by sexual selection (in fact, traits favored by sexual selection may often occur at the expense of longevity; Brooks, 2000). In our simulations, however,

reproduction was possible over the entire lifespan, and natural selection had no other traits to select upon. A more realistic scheme would provide for alleles that have different effects upon the survival of a replicator at different points in its life history. Thus, selection would have to confront the tradeoff between peak fitness in youth and longevity, which is often viewed as the evolutionary basis for senescence (Medawar, 1952). Due to the declining strength of selection pressure on later-acting genes, this tradeoff has been shown to predict not only senescence, but also the existence of mortality functions resembling those found in actual populations (Mueller & Rose, 1996).

Finally, the model presented here might seem to predict that males age more slowly than females, whereas the opposite has been argued to occur among real animals (Rossler, Kloeden, & Rossler, 1995; Brooks, 2000; Daly and Wilson, 1983). This difference may reflect the absence of several mechanisms in the simulation: (1) alleles affecting fitness at different points in the lifespan, as already mentioned, and (2) agonistic interactions among males, requiring costly physiological specializations. It has sometimes been asserted that parental investment theory unequivocally predicts the evolution of faster senescence among males (Trivers, 1968), but the arguments for this conclusion do not appear compelling. More complex simulations might shed new light on this issue. It is not intuitively obvious (to the authors at least) how male and female lifespans would evolve if the simulation described here were altered to include multiple fitness alleles with different effects on survival and fecundity at different points in the replicators' life history (as in Mueller & Rose, 1996).

Another obvious and important extension of the present work would be to include in the model genes that direct male resources into parental care. The framework described here might also prove useful in exploring the adaptive basis for a number of mating strategies and phenomena (such as nuptial giving in insects) whose evolutionary significance remains controversial among biologists.

Conclusions.

Simulated evolution of sex-linked fitness and mating selectivity traits confirms that greater female reproductive refractoriness alone suffices to drive the evolution of greater selectivity in female as compared to male mating choices. This happens even when the females do not have the opportunity to choose the best available mate from a number of simultaneously presented, or even to adjust their mate-selection criteria according to experience. The results also showed an unexpected instability in the evolved distribution of female responses to low-fitness mates with moderate-sized breeding populations. The framework described here provides a simulation platform that is simple and potentially useful in examining a variety of controversial questions regarding the evolutionary consequences of parental investment and the evolution of sex differences².

² For source code (in C++), contact the first author.

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Parameter	Description	Value in Figures 1-3
Initial Population Size	(Remains stable; see text.)	1000
Number of Timesteps Simulated		150,000
Female reproductive refractoriness	Number of time steps before female can mate again	4 timesteps
Male reproductive refractoriness	Number of time steps before male can mate again	0 (no refractoriness)
Lifespan	Lifespan of short- and long-lived variants	15 and 25 timesteps
Longevity mutation rate	Prob. of switching longevity feature bit in offspring	0.01
Selectivity mutation Rate	Standard deviation of Gaussian error added to selectivity parameter of offspring	.005

FIGURE CAPTIONS

1. Proportion of long-lived males and females in the population in a run of 150,000 timesteps with the parameters specified in Table 1. Slightly higher average male longevity proved robust across variations in parameter values.
2. Changes in selectivity of males and females in two runs of the simulation with the parameter values specified in Table 1. “Male mate|0” = average probability a male will mate with a short-lived prospective mate; “Female mate|1” = average probability a female will mate with a long-lived prospective mate; etc. While distributed identically at the outset of the simulations, female selectivity evolved to exceed male selectivity.
3. Average selectivity values over 16 simulations with parameters described in Table 1. The error bars indicate the standard deviation of each parameter; symbols refer to the sex of the replicators whose selectivity is represented.
4. Effect of the duration of female reproductive refractoriness (in timesteps) on the average probability of females mating with short-lived mate at 150,000 timesteps, averaged over three runs at each refractoriness value.







